SPECIAL ARTICLES

BIOLOGICAL CONCLUSIONS DRAWN FROM THE STUDY OF THE TITANOTHERES[1]

THE chief object of this communication is to point out a possible harmony between the "continuity" and "discontinuity" theories of the phenomena of development.

The titanotheres, as an extinct family of mammals extending from the summit of the Lower Eocene to the summit of Lower Oligocene times, offer an exceptional opportunity for the solution of the two chief modern questions of evolution: first, the mode of transformation of existing characters; second, the mode of origin of new characters. The material available is now the most complete of any extinct family of mammals, embracing several nearly continuous series which branch out into a large number of phyla, some of which may be carried through all the phases of transformation. The investigation has been carried on with the aid of Dr. W. K. Gregory, and is marked by the introduction of a very exact system of measurements, whereby the various kinds of transformation may be studied in numerical terms. This exhaustive research appears to have a significant bearing upon the diverse theories of transformation entertained by the two modern schools of thought, the zoological and botanical, and the paleontological.

From the time of Waagen in 1869, who introduced the term "mutation" for the *stages* of the continuous development of certain inconspicuous but genetically important characters in Ammonites, the idea of continuity has become the established law among paleontologists. Neumayr added the conception of "*Mutationsrichtung*," that is, of trend or direction of development. The researches of Hyatt and Beecher were directed rather to the phenomena of recapitulation than specifically to the phenomenon observed by Waagen. Their writings, however, bring volumes of testimony to the law of continuity of development. This law has been established among vertebrates as well as invertebrates. The nature of the evidence presented to the paleontologist is entirely different from that presented to the zoologist; as an observer the former is practically immortal, that is, his range of observation, where it is possible to assemble continuous series of organisms, extends over enormous periods of time in contrast to the fleeting and essentially mortal glimpses which the botanist and zoologist may obtain of the fundamental processes of transformation.

Over against the idea of continuity, of definite development, and of certain trends of evolution, there have been developed among the students of living animals and plants (Bateson, de Vries and others) the notion of discontinuity and of order or orderly development produced only by selection. To this discontinuity de Vries has unfortunately applied the same term "mutation" which was introduced into biological literature by Waagen with entirely different significance; the name *saltation* should be attached to the de Vries hypothesis; until this is done we must speak of "mutations of Waagen" and "mutations of de Vries." The discontinuity conception has been strengthened rather than weakened by the wonderful revelations of Mendelian heredity, including the doctrine of unit characters and of "alternate inheritance."

The only tenet which the "continuous" and "discontinuous" schools of thought hold in common, or rather have reached in common, is that germinal evolution is the chief phenomenon upon which our attention must be concentrated. In the present communication the phenomena resulting from somatic changes or ontogeny, from environment, and from selection may be left out of consideration, and we may direct our thought solely and exclusively upon germinal evolution as it is displayed in the origin of new characters and in the transformation of existing characters in the titanotheres.

In all the sequence of the titanotheres only four kinds of change are observed: (1) *Increase of size.* This happens to be an almost

[1] Abstract of paper presented at the meeting of the National Academy of Sciences, Washington, April 19, 1911. Based upon the author's monograph "The Titanotheres," in preparation for the U. S. Geological Survey.

universal principle in this family, although it is by no means universal among mammals nor even among the Herbivora. (2) *Loss of parts.* This plays a very small part in the series of titanotheres as compared, for example, with the horses, since the chief parts lost are one element in the carpus, the trapezium and certain upper and lower incisor teeth. (3) *Changes of proportion.* This comprehends one of the most important and significant parts of titanothere evolution. Such change it is proposed to designate as "allometric," and new parts originating in this way may be termed "allometrons." (4) Continuous definite or *adaptive origins* of new characters, which the writer has previously termed "rectigradations."

Of the above phenomena (1) increase of size and of (2) loss of parts may be left out of consideration, and attention may be directed upon the (3) *allometrons* and the (4) *rectigradations.* It is found at once that their mode of appearance or the laws governing them are definite.

First, as to *rectigradations,* as exemplified by new cusps upon the teeth or by newly arising horns upon the skull, we find them subject to four important principles: (1) Rectigradations appear under the law of ancestral hereditary control, that is, the same rectigradations arise independently at different times in the descendants of remote common ancestors. This law has already been enunciated at a previous meeting of the academy and constitutes one of the most important generalizations brought out by the study of the titanotheres. (2) Rectigradations are continuous, arising from infinitesimal and almost invisible beginnings and passing into a stage of usefulness; this principle was pointed out many years ago by the author and described as "definite variation." (3) Rectigradations from the time of their first appearance are subject to the allometric influence of surrounding parts; thus a horn arising as a rectigradation in a brachycephalic skull will assume from the beginning a rounded form; arising in a dolichocephalic skull it will assume an elongate or oval form. (4) It is probable, but has not yet been demonstrated, that rectigradations are subject to fluctuations, that is, are more or less strongly developed around an average mean.

Second, the *allometrons* or changes of proportion follow partly the same and partly different laws than those pursued by the rectigradations. The most fundamental difference is the following: allometrons arise independently of remote ancestral hereditary control, that is, from a mesaticephalic ancestor there may arise, on the one hand, a dolichocephalic, and, on the other hand, a brachycephalic descendant; when, however, a trend of development, a law which appears to be coincident with the "*Mutationsrichtung*" of Neumayr, is once established then a tendency toward brachycephaly or dolichocephaly, respectively, becomes increasingly manifest; in this sense allometrons resemble rectigradations. The second law is that allometrons are continuous. This is positively demonstrated in certain phyla, and apparently will be demonstrated in all the phyla as soon as a full series or sequence is obtained. Any other theory of change of proportion but continuity is untenable in the face of the hundreds of measurements which especially demonstrate progressive brachycephaly. Measurements demonstrating progressive dolichocephaly and cytocephaly, or the bending down of the facial upon the cranial region of the skull, are based on less complete series.

It has been found convenient to introduce a series of cephalic indices of the ratios between breadth and length similar to the cranial indices used in anthropology. Thus, breadth $\div$ length gives the cranial index of a titanothere, and the gradual transformation from mesaticephaly into brachycephaly or dolichocephaly may be expressed in exact numerical terms. Every bone of the skull enters into these remarkable transformations, and every single bone has its own individual percentage of increment. The evolution of every part is differential. Thus there is no general stretching of the skull in dolichocephaly, as if it were composed of india rubber; the elongation may be confined to cer-

tain regions. It has recently been found that the ancestral titanotheres are dolichocephalic, of the type known as proöpic-dolichocephaly because the chief elongation is in front of the orbital region. Their descendants are also dolichocephalic, but the type is opisthopic dolichocephaly, that is, the chief elongation is behind the orbital region.

Similar allometric indices are also found in the limbs. For example, the ratio of the length of the tibia to that of the femur is very significant and is constantly changing in adaptation to weight and to speed.

Considering the transformation of the titanotheres in comparison with that of the horses and many other lines of mammals, where successive series have been obtained, we observe again exactly similar phenomena. It *appears that the law of continuity, of orderly and in a sense of predetermined transformation can now be established beyond refutation.*

The question then arises whether these laws of "continuity" can be harmonized with the potent demonstration that certain new characters and certain new proportions arise as saltations or discontinuously. The hypothesis which is here advanced is that continuity is the normal mode of development under natural conditions, that there are certain definite trends or tendencies, that there is in continuous series a "*Mutationsrichtung,*" that by this continuous development the greater number of so-called "unit characters" have arisen, that occasionally, however, new unit characters may and do arise suddenly. The hypothesis may be expressed as follows: that the normal development of unit characters is a continuous progress, that under certain abnormal conditions, as of sudden change of environment, certain new unit characters may appear suddenly, that the cross-breeding of pure natural races in which unit characters have been built up by continuous processes breaks up these unit characters into a mosaic and gives rise to the larger part of the apparently saltatory or discontinuous phenomena which are being observed by the modern experimentalists.

As illustrations of this hypothesis, take as a very simple one the transformation of the head form in various human races; the development of dolichocephaly and of brachycephaly has in all probability been by continuous transformation in one direction or the other. In support of continuity is the evidence adduced among the titanotheres. When dolichocephalic and brachycephalic races intermingle, the fact that dolichocephaly or brachycephaly is a unit character appears at once in the non-blending of head form subject to the law of alternate inheritance. Another illustration is afforded by the results of the interbreeding of pure stocks of the horse, namely, according to the observations of Ewart, the Arab, or plateau type, the Przewalsky, or steppe type, and the draught, or forest type. Each of these pure original stocks apparently acquired by gradual transformation a very large number of distinctive characters displayed in the head, in the teeth, in the backbone, in the limbs, and last but not least in the psychic activities of these three great strains which have been bred for ages among very diverse environmental conditions. As soon as these three pure stocks are intermingled the fact that each is a mosaic of an enormous number of single, or unit characters becomes apparent in the mosaic type of horse which is produced, a horse showing singly or in groups various unit characters of the plateau, steppe or forest types. The transformation which, for example, has built up respectively the slender cannon bones of the desert and heavy cannon bones of the forest type has been, we have every reason to believe, a continuous, or progressive, or allometric change. On interbreeding, these slender or massive proportions may partly blend or may be detached as "units" from the progressively slender or massive head types to which they belong.

By far the greater number of the experiments carried on in support of the theory of discontinuity have been among hybrids, crossed strains, artificial strains, or strains subjected to unnatural changes of environment. It is important, therefore, for experimentalists to extend their work among abso-

lutely pure, natural races. Wherever nature is experimenting, as discerned by the field zoologist in the observation of geographic series from east to west, and north to south, from humid into arid regions, we are repeatedly finding geographically continuous series which shade into each other in color, in skull proportion, and limb proportion, and all other characters by continuous degrees of change.

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UNDERGROUND TEMPERATURES

IT is an established fact that as the earth is penetrated below the limit of seasonal changes the temperature is invariably found to rise. Observations made in deep borings, wells, tunnels and mines have been sufficiently numerous over the earth's surface to indicate that the rise of temperature with depth "can not be explained on mere local causes." The rate of temperature increase is not uniform but is found to be quite variable, not only in different localities, but frequently in the same boring. This variation of heat increment is doubtless due to a number of causes,[1] such as differences in the thermal conductivity of rocks which vary in lithologic character, structure and contained water; inequalities of topography; circulation of water; chemical action; compression, etc. Whether the heat increment observed in the superficial zone continues to the center of the earth is not known, as observations are limited to only a little more than 1/4,000 of the earth's radius. Some investigators regard it as more probable that the rise of temperature diminishes below the superficial zone.

The conducting power of rocks was first accurately measured by Forbes,[2] and later by others. Forbes found that trap rock was the poorest conductor and solid sandstone the best. Sir Archibald Geikie[3] says, "the lighter and more porous rocks offer the greatest resistance to the passage of heat, while the more dense and crystalline offer the least resistance." The British Association Committee on Thermal Conductivities of Rocks[4] expressed the resistance of quartz by the number 114, basalt by 273, and cannel coal by 1,538. The same authority[5] records that heat travels four times as fast in foliated rocks, such as slate and schist, in the direction of cleavage than across it. It has been shown also that thermal resistance is lowered by the presence of interstitial water.

The subject of underground temperature attracted attention as early as nearly two centuries ago, when observations were made in the mines of Alsace by Gensanne in 1740, who found an increase of 1° F. in 50 feet. Among some of the earlier observers may be mentioned Saussure, Humboldt, Daubuisson, de Tebra, Forbes and Fox, Henwood, Cordier, De la Rive and Marcet, Phillips and others.

From 1868 onwards the British Association Reports contain valuable contributions by the committee on underground temperatures, and a summary is published in the volume for the year 1882. In 1886 Professor Prestwich's[6] valuable contribution on the subject of underground temperatures appeared, in which he collated all available data up to that time. This paper was later revised and published in his "Collected Papers on some Controverted Questions of Geology," 1895, pp. 166–279. Observations have been made and data bearing on this subject have been contributed at intervals to the literature from 1886 to the present time, with the conclusion that while there is an undoubted increase in temperature downward, the rate is more variable than was at first supposed.

Professor Prestwich gave the number of different localities and mines where observations were recorded as 248, and the number of stations 530. He found, with but few excep-

[1] Chamberlin and Salisbury, "Geology," Vol. I., 1904, pp. 544–547; Geikie, A., "Text-book of Geology," Vol. I., 4th ed., 1903, pp. 63–64.

[2] *Trans. Roy. Soc. of Edinburgh*, Vol. XVI., p. 211.

[3] "Text-book of Geology," 4th ed., 1903, Vol. I., p. 63.

[4] Rept. Brit. Asso. Adv. of Science, 1875, p. 59.

[5] *Ibid.*, p. 61.

[6] *Proc. Roy. Soc. of London*, 1886, Vol. XLI., pp. 1–116.